SPECIES-DISTINCTIVENESS OF LONG-BILLED DOWITCHER SONG (AVES: SCOLOPACIDAE)

E. H. Miller, W. W. H. Gunn*, J. P. Myers, and B. N. Veprintsev

Abstract.—A prominent type of breeding vocalization ("song") of the Longbilled Dowitcher (Limnodromus scolopaceus) is described and compared with song of the Short-billed Dowitcher (L. griseus). In L. scolopaceus, the song consists of an introductory series of elements followed by several identical components ("song units"), each consisting of two element types in series. The first type is a doublet, and the second is a buzz. Song of L. griseus is organized similarly, but each song unit has three element types in series and no doublets. The species differ strongly in quantitative features of buzzy elements. Analyses of vocalizations of the Asiatic Dowitcher (L. semipalmatus), and of other groups within the Scolopacidae (especially godwits, woodcock, and snipe) are needed to evaluate the systematic significance of these observations.

Acoustic signals provide useful characters for systematic studies on birds, particularly closely related species (e.g., Stein 1963; Lanyon 1978; Mundinger 1979; Johnson 1980). This is likely to apply to sandpipers and their allies (Scolopacidae, 86 species), though little research on acoustic communication in the group has been carried out. Sounds of many species are quite distinctive and vary relatively little intraspecifically (Miller 1984). Such sounds may provide insight into affinities of several problematic taxa, including dowitchers (Limnodromus). This genus consists of three species whose affinities with calidridine sandpipers, godwits, snipe, and woodcock remain unclear (Pitelka 1950; Strauch 1976, 1978; our nomenclature and classification follow Gochfeld et al. 1984). The purpose of this paper is to describe one prominent type of vocalization ("song") used by the Longbilled Dowitcher (L. scolopaceus) during breeding, and compare it with the homologous call type of the Short-billed Dowitcher (L. griseus). These two species are much more closely related to one another than either is to the Asiatic Dowitcher (L. semipalmatus), whose vocalizations have not been analyzed; song of L. griseus is described elsewhere (Miller et al. 1983), as are other calls of L. scolopaceus (Tikhonov and Fokin 1979, 1980, 1981). For general accounts of the species, see Johnsgard (1981) and Cramp (1983).

Methods and Materials.—Records were obtained near Barrow and Atkasuq, Alaska in June 1977, and at Berelyakh, near the mouth of the Indigirka River, Yakutiya, U.S.S.R., in June 1976. Analyses were made with a Kay Elemetrics Sona-Graph 7029A, and a Honeywell Visicorder System 1858. Variables were measured on wide-band (300 Hz) sound spectrograms; even the frequency measure used (terminal frequency of certain elements) was more easily and repeatably measured on wide- than on narrow-band (45 Hz) spectrograms. Variables used for each song unit were (see below and Figs. 1 and 3 for terminology): (i) interval preceding song unit (this was the interval between one unit's type c element and the next unit's type a element, or the interval between a song's introduction and

* Deceased.

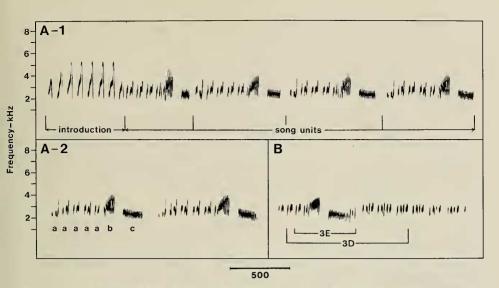


Fig. 1. Sound spectrograms of song of *L. scolopaceus*. A (two parts), Song from Alaska, consisting of an introduction and six song units (A-2 shows the continuation of A-1). Element types are indicated for the first song unit in A-2; B, Terminal song unit in song from the U.S.S.R., with following compound elements. Segments marked as 3D, 3E are shown as oscillograms in Fig. 4D, E, resp. Analyzing filter bandwidth, 300 Hz; time marker in msec.

the first type a element); (ii) total duration of song unit; (iii) duration of the series of type a elements; (iv) duration of type b and c elements; (v) rate of frequency modulation of type b and c elements (estimated using up to the first 10 cycles in the elements); and (vi) terminal frequency of type b and c elements.

Results. —Song of L. scolopaceus consists of an introduction, followed by several repetitions of a complex sequence ("song unit"). The introductory portion is a sequentially graded series of brief elements, each with a broad frequency range, and each typically increasing then decreasing quickly in frequency (Fig. 1A). Two element types occur in fixed sequence in each song unit: (a) doublets, occurring as a sequentially graded series of variable length; and buzzes, the first (b) being brief, and the second (c) longer and lower in frequency (Figs. 1, 3). The sequence and general characteristics of element types in L. scolopaceus song were present in all song units examined, from Alaska (n = 10) and the U.S.S.R. (n = 12). Song of L. griseus also consists of an introductory series, followed by several song units, but three distinct element types occur in each song unit (Fig. 2). In addition, the number of buzzy elements is variable, ranging from one to five (Fig. 2; Miller *et al.* 1983).

The parts of each doublet in L. scolopaceus song have a simple structure which changes gradually over a sequence: the first part rapidly increases in frequency then levels off; the second may show a similar pattern, or a more complex one of rises then falls in frequency (Fig. 3C). The amplitude envelopes of type a elements are simple and consistent, and the parts are roughly equal in peak amplitude (Fig. 4). Type b elements begin with one or more modified type a elements (e.g., Figs. 3, 4), but are dominated by a rapid frequency modulation of

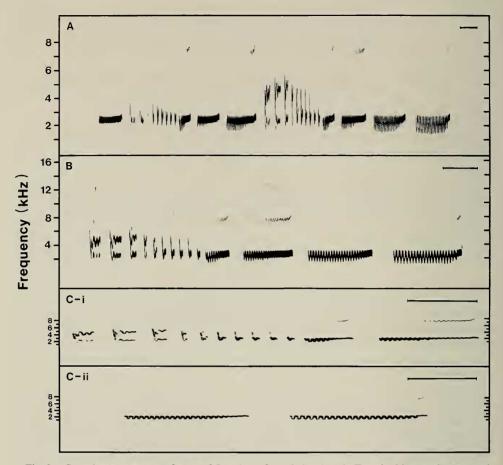


Fig. 2. Sound spectrograms of song of *L. griseus* from Labrador. A, Terminal buzzy element and two complete song units. Analyzing filter bandwidth, 300 Hz; B, Second song unit from panel A, shown on a different time scale. Analyzing filter bandwidth, 300 Hz; C (two parts), Same song unit as B, shown on different frequency and time scales. Analyzing filter bandwidth, 45 Hz. Time markers, 125 msec.

a gradually increasing carrier frequency (Figs. 1, 3). The modulated part of b elements averages about 80 msec long, with a modulation rate of about 100 Hz and a terminal frequency of about 3 kHz; they are significantly briefer, more slowly modulated, and higher in frequency than in *L. griseus* (Table 1). Type b elements have the highest amplitude in a song unit, and show pronounced modulation of amplitude coupled to that of frequency, as in *L. griseus* (Fig. 4; Miller *et al.* 1983). Type c elements are simply buzzes with a slowly descending carrier frequency (Figs. 1, 3). They average about 145 msec long, have a modulation rate of about 94 Hz, and a terminal frequency of about 2 kHz; thus they are briefer, more slowly modulated, and slightly lower in frequency than comparable elements of *L. griseus* (Table 1). Unlike type b elements, rhythmic amplitude modulation of c elements is not pronounced (Fig. 4). Type c elements are both absolutely and relatively briefer and lower in frequency (compared to type b elements) in *L. scolopaceus* than in *L. griseus* (Table 1).

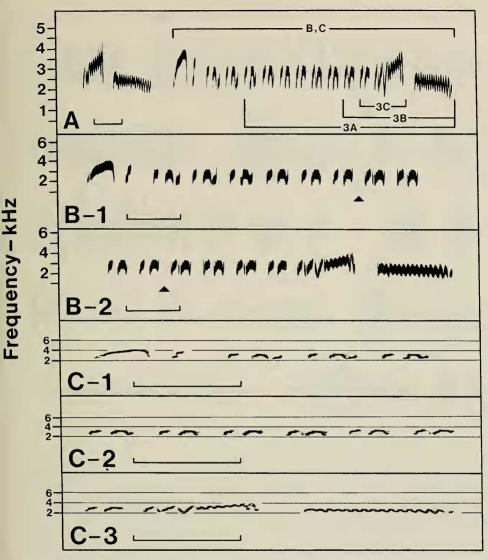


Fig. 3. Sound spectrograms of song of *L. scolopaceus*, A, Terminal elements (types *b*, *c*) of one song unit, followed by an entire song unit, from an Alaskan song. The song unit marked "B, C" is also shown in parts B and C of this figure. Other segments marked are shown as oscillograms in Fig. 4A, B, C. Analyzing filter bandwidth, 300 Hz; B (two parts), Same song unit as in A, shown on a different time scale. There is some overlap between parts 1 and 2; the triangles mark the same point in the series of *a* elements. Analyzing filter bandwidth, 300 Hz; C (three parts), Song unit as in A and B, shown on a different time scale and with different analyzing filter bandwidth (45 Hz). The last element in each part is followed by the first element in the part immediately below; there is no overlap. Time markers, 125 msec.

A call type often associated with song consists of rhythmically repeated groups of brief simple elements (Figs. 1B, 4D); these are very similar in structure to a call type of several calidridine species (Miller 1983a, b).

Major differences between song of L. scolopaceus and L. griseus include: the

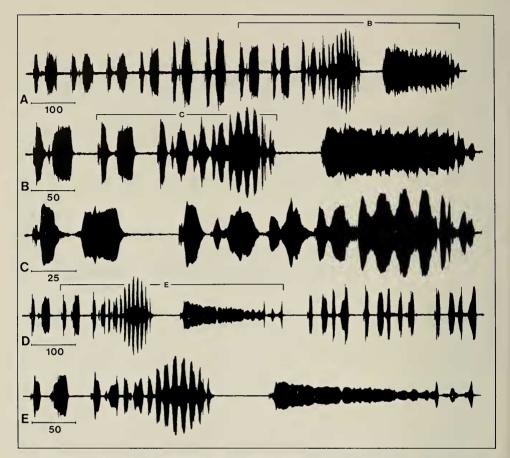


Fig. 4. Oscillograms of song of *L. scolopaceus*. A, B, C, Segments of a song unit from an Alaskan song, shown at different time scales (refer to Fig. 3A). The portions marked "B" in part A, and "C" in part B, represent parts B and C of this figure; D, E, Segments of a song unit with following elements, in song from the U.S.S.R., shown at different time scale (refer to Fig. 1B). The portion marked "E" in part D represents part E of this figure. Scale for amplitude varies across traces, but is constant within single groups; time markers are in msec.

presence of doublets in the former, whereas the latter has series of two kinds of elements at a comparable position in each song unit; temporal and frequency characteristics of buzzy elements; low number of buzzy elements in *L. scolopaceus*; and weakly developed amplitude modulation in type *c* elements of *L. scolopaceus*.

Discussion

Songs of *L. scolopaceus* and *L. griseus* show many quantitative and some qualitative differences, but are very similar in hierarchical organization and in characteristics of buzzy elements. Both species differ strongly from *L. semipalmatus*, which utters repeated low-frequency, buzzy elements during aerial song (Veprintsev 1982). The buzzy elements in song of *L. griseus* and *L. scolopaceus* are strikingly similar to those in song of a calidridine, the Least Sandpiper (*Calidris*)

Table 1.-Summary of descriptive statistics for variables on song units of Limnodromus scolopaceus and L. griseus.^a

Variable	L. scolopaceus ^b	L. griseus ^c	Pª
Interval preceding song unit	*68.7 ± 5.37	69.5 ± 1.79	NS
(msec)	(18)	(63)	
Duration of song unit (msec)	824 ± 53.6	986 ± 32.8	*
	(15)	(69)	
Duration of buzzy elements (ms	sec)		
a. First element	78.8 ± 2.33	112 ± 4.2	***
	(19)	(83)	
b. Second element	**145 ± 10.2	240 ± 6.1	***
	(18)	(83)	
c. [(b - a)/a]%	84.8 ± 12.29	139 ± 9.4	*
	(18)	(82)	
Initial cycle rate of buzzy elements (Hz)			
a. First element	101 ± 1.1	140 ± 1.1	***
a. Thist clement	(19)	(82)	
b. Second element	94.3 ± 1.94	(62) 114 ± 1.1	***
	(18)	(85)	
c. [(b - a)/a]%	-6.77 ± 2.205	-18.7 ± 0.82	***
	(18)	(80)	
Terminal frequency of buzzy		()	
elements (Hz)			
a. First element	2977 ± 24.2	2424 ± 10.3	***
A CONTRACTOR OF	(19)	(86)	
b. Second element	***2207 ± 36.1	2342 ± 18.2	**
	(18)	(85)	
c. $[(b - a)/a]\%$	***-25.7 ± 1.47	-3.50 ± 0.732	***
	(18)	(81)	
Interval between first two	*66.6 ± 2.26	56.5 ± 1.24	***
buzzy elements (msec)	(18)	50.5 ± 1.24 (84)	
buzzy clements (msec)	(10)	(04)	

^a Each cell entry is listed as $\overline{Y} \pm SE(n)$.

^b Variables which differ significantly between samples from Alaska and the U.S.S.R. are indicated by asterisks (* P < 0.05, ** P < 0.01, *** P < 0.001; by one-way analyses of variance).

^c Data are from Table II of Miller et al. (1983), or from raw data used in that study.

^d Probability of difference between means (two-tailed), based on *t*-tests (symbolism as for footnote b; NS = not significant (P > 0.05)).

minutilla; Miller 1983a), notably in their sequential increase in duration and decrease in frequency and modulation rate within song units, and their rhythmic amplitude and frequency modulation (which are coupled). Other features of song structure in these three species are similar, but none so strikingly. Information about songs of other calidridines is too scanty to permit comprehensive comparisons, though song in several species is very different (Miller 1983b).

Vocalizations of only two species each of snipe, woodcock, and godwits have been analyzed, and these differ strongly from song structure described here (Glutz von Blotzheim et al. 1977; Mal'chevskii 1980; Warham and Bell 1980; Cramp 1983; Miller 1984). However, buzzy elements occur in several of the taxa mentioned, and also characterize nuptial displays in several species of Calidridini (Miller 1983b). Quantitative analysis of buzzy elements which occur within song, or independently of it, could therefore provide insight into adaptive radiation and affinities of this group of Scolopacidae. Available evidence is clearly too limited to judge which features of *L. scolopaceus* song are ancestral and which are derived. Detailed descriptions of vocalizations in the taxa mentioned are badly needed.

Acknowledgments

We thank F. A. Pitelka, B. McCaffrey, and T. Hall for assistance. Recordings in Alaska were obtained during ecological research funded by the United States Department of Energy in contracts to F. A. Pitelka. Other research support was from the Natural Sciences and Engineering Research Council of Canada (individual operating grant to E. H. Miller), and the Friends of the British Columbia Provincial Museum (equipment and research grants to E. H. Miller).

Literature Cited

- Cramp, S. (ed.) 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, Vol. 3.-Oxford University Press, Oxford, 913 pp.
- Glutz von Blotzheim, U.N., K. M. Bauer, and E. Bezzel (eds.). 1977. Handbuch der Vögel Mitteleuropas, Band 7, Charadriiformes (2. Teil).-Akademisch Verlagsgesellschaft, Wiesbaden.
- Gochfeld, M., J. Burger, and J. R. Jehl, Jr. 1984. The classification of the shorebirds of the world. Pp. 1-15, *in* J. Burger and B. L. Olla, eds., Behavior of marine animals, Vol. 5, Shorebirds: breeding behavior and populations.—Plenum Press, New York.
- Johnsgard, P. A. 1981. The plovers, sandpipers, and snipes of the world.-University of Nebraska Press, Lincoln, 493 pp.
- Johnson, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). University of California (Berkeley) Publications in Zoology 112:1–151.
- Lanyon, W. E. 1978. Revision of the *Myiarchus* flycatchers of South America.-Bulletin of the American Museum of Natural History 161:427-628.
- Mal'chevskii, A. S. 1980. (New data on sound communication in birds).—Vestnik Leningrad University Biology 4:58-64 [in Russian].

Miller, E. H. 1983a. Structure of display flights in the Least Sandpiper.-Condor 85:220-242.

-----. 1983b. The structure of aerial displays in three species of Calidridinae (Scolopacidae). -- Auk 100:440-451.

— 1984. Communication in breeding shorebirds. Pp. 169-241, in J. Burger and B. L. Olla, eds., Behavior of marine animals, Vol. 5, Shorebirds, breeding behavior and populations. – Plenum Press, New York.

W. W. H. Gunn, and R. Harris. 1983. Geographic variation in aerial song of the Shortbilled Dowitcher (Aves, Scolopacidae).—Canadian Journal of Zoology 61:2191–2198.

- Mundinger, P. 1979. Call learning in the Carduelinae: Ethological and systematic considerations.— Systematic Zoology 28:270–283.
- Pitelka, F. A. 1950. Geographic variation and the species problem in the shore-bird genus Limnodromus.-University of California (Berkeley) Publications in Zoology 50:1-108.
- Stein, R. C. 1963. Isolating mechanisms between populations of two populations of Traill's Flycatchers.—Proceedings of the American Philosophical Society 107:21-50.
- Strauch, J. G., Jr. 1976. The cladistic relationships of the Charadriiformes. Ph.D. thesis, University of Michigan, Ann Arbor.
- ———. 1978. The phylogeny of the Charadriiformes (Aves): A new estimate using the method of character compatibility analysis.—Transactions of the Zoological Society of London 34:263– 345.
- Tikhonov, A. V., and S. Yu. Fokin. 1979. (Acoustic signalling and the behavior of shorebirds in early ontogenesis. I. Prenatal stages of development).—Nauchnye Doklady Vysshei Shkoly Biologicheskie Nauki 10:33-40 [in Russian].

 -. 1980. (Acoustic signalling and behavior of shorebirds in early ontogenesis. II. Signalling and the behavior of nestlings).—Nauchnye Doklady Vysshei Shkoly Biologicheskie Nauki 10:45– 54 [in Russian].

 . 1981. (Acoustic signalization and behavior during the nesting period in snipe). — Byulleten' Moskovskoga Obshchestva Ispytatelei Prirody Otdel Biologicheskii 86:31-42 [in Russian].

Veprintsev, B. M. 1982. (Birds of the Soviet Union. A sound guide). (2 long-playing discs). – All-Union Studies for Recorded Sound. U.S.S.R. [notes and narration in Russian].

Warham, J., and B. D. Bell. 1980. The birds of Antipodes Island, New Zealand. – Notornis 26:121– 169.

(EHM) Vertebrate Zoology Division, British Columbia Provincial Museum, Victoria, B.C. V8V 1X4, Canada, and Biology Department, University of Victoria, Victoria, B.C. V8W 2Y2, Canada. (WWHG) Box 738, Bobcaygeon, Ontario K0M 1A0, Canada. (JPM) Vertebrate Biology, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A. (BNV) Institute of Biological Physics, U.S.S.R. Academy of Sciences, Pushchino-on-Oka, Moscow Region 142292, U.S.S.R.